# Density-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in Placentia Bay, Newfoundland

## David Robichaud and George A. Rose

Age 0 cod (*Gadus morhua*) were surveyed with beach-seines monthly from September to December, 1997−1999, at sites located throughout Placentia Bay, Newfoundland. Catch rates (densities) varied annually, being highest in 1998 (7 fish per sample) and lowest in 1997 (<1). Each year, fish size and density increased from September to November, as expected from a stock that tends to produce a single cohort spawned in April/May. However, in December the expected larger fish were absent, and the presence of smaller cod suggested a later cohort (July spawning). Large-scale spatial patterns also persisted among years, with densities consistently higher in the inner bay and on the western side, and lower on the eastern side. The rank of the sites from greatest to lowest density of age 0 cod remained fairly consistent among years. In a comparison of all 12 sampling events, the proportion of sites occupied by cod was strongly and positively correlated with the total number caught ($r^2 = 0.95$). These observations suggested a density-dependent range expansion not previously reported for age 0 cod.

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## Introduction

The strength of Atlantic cod (*Gadus morhua*) year classes that will eventually recruit to fisheries correlates more closely with their abundance at the demersal juvenile stage than at earlier life stages (Sundby *et al.*, 1989; Bradford, 1992; Helle *et al.*, 2000, and references therein). Hence, on the northeast coast of Newfoundland, several attempts have been made to understand better the abundance and spatial dynamics of juvenile cod (Anderson and Dalley, 1997; Schneider *et al.*, 1997; Anderson and Gregory, 2000). Similar work has been conducted on Georges Bank (Lough *et al.*, 1989) and elsewhere. In most previous studies, largely on depleted stocks, the importance of specific habitat types to demersal juvenile cod has been reported and emphasized (Tupper and Boutilier, 1995; Gotceitas *et al.*, 1997). Range expansion/contraction with changing abundance (i.e. density-dependence) has been explored (Schneider *et al.*, 1997), but it has not been demonstrated.

The cod stock off the south coast of Newfoundland is currently regarded as being in the best condition of the West Atlantic cod stocks (from West Greenland to Georges Bank), and supports the largest cod fishery in the region

(Brattey *et al.*, 2003). Placentia Bay, which is the centre of the fishery, has sustained from one-third to one-half of the total catch since the reopening of this fishery in 1997 (a moratorium was in place from 1993 to 1996). Studies of cod spawning and adult distribution and migration have been ongoing in Placentia Bay since 1996 (Lawson and Rose, 1999, 2000a, b; Bradbury *et al.*, 2000; Robichaud and Rose, 2001, 2002a,b, 2003; Mello and Rose, 2005). Cod spawn each spring in Placentia Bay, especially in the vicinity of the Bar Haven Island shoals (Figure 1), but also in the outer bay off Cape St Mary's and Oderin Bank (Lawson and Rose, 2000a). Spawning peaks from April to June, and eggs and larvae appear to drift southwestwards towards the open sea (Bradbury *et al.*, 2000). The Placentia Bay cod have been identified as a coastal population with spatial, temporal, and possible genetic properties separate from adjacent cod groups (Ruzzante *et al.*, 1998; Brattey *et al.*, 1999, 2003; Lawson and Rose, 2000a, b).

The purpose of this study was to identify potential nursery sites within the bay, and to test whether sites were consistent from year to year. We also tested for density-dependence of juvenile cod distribution, under the null hypothesis that changes in abundance would not result in changes in
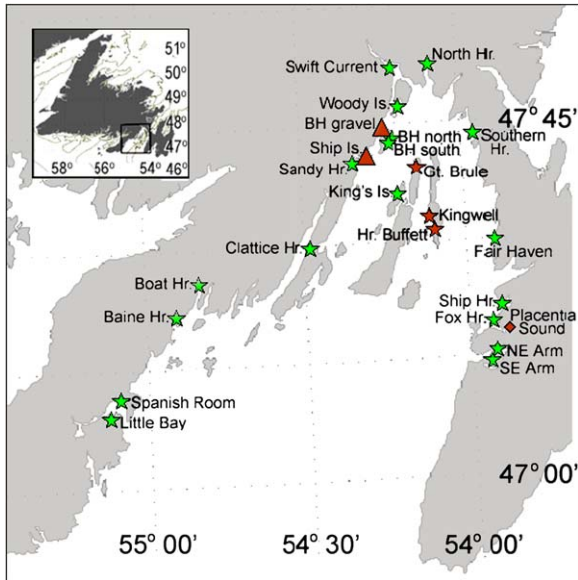
Figure 1. Map of Placentia Bay, showing the location of the 18 sites sampled in all three years (lightly shaded stars), the three eelgrass sites added in 1998 (dark shaded stars), the two sites with gravel substratum (triangles), and the site (Placentia Sound) used only in some of the analyses (diamond). Note that the position of Bar Haven North has been displaced to the northeast for presentation purposes, so it could be distinguished on the map from Bar Haven South. Bar Haven is abbreviated to BH. Inset: the island of Newfoundland, with box showing location of the Placentia Bay study area.

occupied range. In addition, we examined the temporal patterns of juvenile density and fish size.

## Material and methods

In 1997, 18 permanent sites were selected covering most of Placentia Bay, and in 1998, five more sites (Figure 1) were added to increase spatial coverage of the eastern and central channels. In October 1998 a 24th site was added. All sites were marked with colourful surveyor's ("flagging") tape to ensure that the same swath was sampled on every visit. Detailed notes describing each site were taken in case the surveyor's tape vanished between sampling periods, and a handheld GPS was used to identify latitude and longitude. Sites covered a variety of habitats, although most contained eelgrass (*Zostera marina*). All sites were sufficiently clear of obstacles to allow the use of a beach-seine.

A complete survey of all sites was conducted monthly from September to December, 1997−1999 (a total of 12 surveys). To make each survey as synoptic as possible, all sites were sampled in as short a period as possible at the start of every month, in an order that was largely determined by weather. Sampling at any site was not confined to a particular tide level or time of day, although all sampling

was done during daylight. Various ancillary variables were recorded along with each beach-seine haul, including eel-grass density, tidal stage, depth, salinity, temperature, and bycatch. The effects of these factors on cod abundance are being examined in a separate study.

At each site, a 25-m beach-seine was hauled by two people towards the shore after being deployed from a small boat. The seine was constructed of knotless nylon mesh, stretched to 19 mm in the wings and belly, and to 12.7 mm in the co-dend. The seine is described in more detail by Lear *et al.* (1980), and its deployment is described in Schneider *et al.* (1997). A standardized area of 880 $m^2$ was sampled on each haul of the seine (16 m alongshore × 55 m offshore) and the net extended up to 2 m off the bottom. Two beach-seine hauls were done in immediate succession. The two seine-haul locations were fixed at each site, approximately 30−100 m apart. The locations were far enough apart to be treated as independent, but close enough to be similar in depth, eelgrass cover, salinity, and exposure. The occurrence of any snags during all hauls was recorded. The standard length of each cod was recorded, and whenever possible, fish were returned alive to the sea.

Analyses were restricted to age 0 cod, because older juveniles (age 1+) were not expected to behave as young-of-the-year in terms of distribution, habitat selection, or feeding behaviour (Dalley and Anderson, 1997; Grant and Brown, 1999). As cod of various age groups were not expected to respond identically to the predictive variables, inclusion of older individuals could potentially have clouded the modelling results. Polymodality in length distributions for each of the 12 bay-wide surveys was used to divide the catch of cod into length classes that corresponded to age groups: age 0 cod were <120 mm, with the majority <95 mm; and age 1 cod were generally between 101 and 215 mm. Cod treated as age 2+ ranged from 199 to 480 mm. Otoliths were taken from cod that died as a result of capture and handling. These otoliths helped define an age−length relationship for very small cod (see Robichaud, 2002). As no larger cod perished, otoliths could not help resolve the fork length "break point" between age 0 and age 1 cod.

### Statistical analyses

The counts of age 0 cod used as the dependent variable throughout most of the analyses were not normally distributed (Shapiro Wilk $W = 0.17$; $p < 0.0001$). They followed more closely the negative binomial distribution (Anscombe, 1950) typical of seine data. The distribution was strongly skewed with a modal count of zero, and a few rare large values. As standard transformation techniques (Sokal and Rohlf, 1995) were not able to normalize the distribution, a maximum likelihood method described in Power and Moser (1999), which followed McCullagh and Nelder (1989), was used to model the relationship between the number of age 0 cod caught and the explanatory variables of interest.

For each model run, $2p$ parameters were estimated iteratively, including the slopes for each of the $p$ explanatory variables (including the intercept; $\beta_1, \beta_2, \ldots, \beta_p$), and each of the negative binomial parameters ($k$ was allowed to be a function of the explanatory variables; $\kappa_1, \kappa_2, \ldots, \kappa_p$).

The negative binomial linear model was adapted for categorical variables using indicator variables (Neter *et al.*, 1996). The significance of variables was determined by comparing the likelihood estimate of a model including the variable of interest with that of a reduced model. Standard deviations of parameters were determined by bootstrapping, because other methods are problematic under a negative binomial error structure (McCullagh and Nelder, 1989; Crawley, 1993; Power and Moser, 1999).

The spatial and temporal trends in the catch of age 0 cod could not be examined using a fully factorial three-way ANOVA on SITE, MONTH, and YEAR because only two hauls were done at each combination of these. Under a standard linear model, two observations per cell would be sufficient, but because the negative binomial model estimates twice as many parameters as the standard linear model, the degrees of freedom become exhausted at less than three observations per cell. The analysis was further complicated by the addition of five sites in the second year of the study, creating a large number of empty cells in 1997. Both problems were overcome by carrying out four separate ANOVAs. The spatial effects (SITE) were evaluated with two separate ANOVAs (one with a single year of data at 18 sites, and another with two years of data at 23 sites), and the temporal effects (YEAR and MONTH) with another pair of ANOVAs (one with three years of data at 18 sites, and another with two years of data at five sites). As four ANOVAs were performed instead of one, alpha was adjusted to account for the inflated probability of type I error. Effects were considered significant at $\alpha' = 0.0125$ (i.e. $\alpha' = \alpha/4$). When YEAR $\times$ MONTH interactions were significant, nested effects were examined. Data for the 24th site were not included because it was only sampled in approximately half the months of the study.

## Results

In 1997, 117 age 0 cod were caught in 144 beach-seine hauls at 18 sites. In each of 1998 and 1999, 184 beach-seine hauls were made at 23 sites. In all, 1266 and 208 age 0 cod were caught in 1998 and 1999, respectively. The average catch rate of age 0 cod was 0.81, 6.88, and 1.13 fish per haul in 1997, 1998, and 1999, respectively. Figure 2 shows the number of age 0 cod caught at each site during the four surveys of the three study years.

### Spatial distribution of catches

Spatial trends in catch of age 0 cod during the first year, and during the last two years were examined with two separate ANOVAs. In both tests, the negative binomial parameter

was not a function of SITE (1997: Dev $= 5.5$; d.f. $= 17$; $p = 0.96$. 1998–1999: Dev $= 21.5$; d.f. $= 22$; $p = 0.49$), so the models were simplified to include only one value of $k$. The simplified models showed that there were highly significant differences in catch among sites in 1997 (among the 18 sites: Dev $= 46.4$; d.f. $= 17$; $p < 0.001$), as well as in the last two years of the study (among all 23 sites: Dev $= 131.0$; d.f. $= 22$; $p < 0.001$). Mean catches at Bar Haven North were significantly higher than all other sites in 1997, and were second only to nearby Great Brule in 1998–1999 (Table 1), a site not sampled in the first year. The sampling sites at King's Island and Ship Harbour also had consistently higher catches of age 0 cod than did other sites. Some sites had consistently small catches of age 0 cod. These included Fair Haven, Swift Current, and Boat Harbour. Overall, the differences in catch among sites were consistent among years (Figure 2, Table 1).

The splitting of the data into two independent sections and ANOVAs allowed one modelled section to be tested against the other. Specifically, the mean predicted catch for the 18 sites during 1997 was significantly correlated with that at the same sites during 1998–1999 ($r_s = 0.53$; $p < 0.05$), and ten of the 18 sites were within two ranks of the predicted value. This confirms that relative abundances were consistent, and can be predicted from these models. In general, sites from the head of the bay and to the west had a greater abundance of juvenile cod than sites on the eastern side of the bay.

### Temporal distribution of catches

Temporal trends in catch of age 0 cod were examined separately for the 18 original sites and for those added in the second year. In both tests, the negative binomial parameter was not a function of MONTH and YEAR (18 sites: Dev $= 9.4$; d.f. $= 11$; $p = 0.58$. Five sites: Dev $= 9.0$; d.f. $= 7$; $p = 0.25$), so the models were simplified to include only one value of $k$. In both cases, the simplified models revealed significant interactions between MONTH and YEAR (18 sites: Dev $= 17.8$; d.f. $= 6$; $p = 0.007$. Five sites: Dev $= 15.9$; d.f. $= 3$; $p = 0.001$). Therefore, the pattern of catch among months in one year did not necessarily correspond to that in other years (Figures 2 and 3). Given the significant interactions, analyses were performed to examine the effects of MONTH within each YEAR.

For the 18 original sites, the negative binomial parameter was not a function of MONTH in any year (1997: Dev $= 2.3$; d.f. $= 3$; $p = 0.51$. 1998: Dev $= 2.2$; d.f. $= 3$; $p = 0.53$. 1999: Dev $= 1.6$; d.f. $= 3$; $p = 0.66$), so the models were simplified to include only one value of $k$. The simplified models showed that the effect of MONTH was significant within all years (1997: Dev $= 21.9$; d.f. $= 3$; $p < 0.0001$. 1998: Dev $= 22.8$; d.f. $= 3$; $p < 0.0001$. 1999: Dev $= 31.2$; d.f. $= 3$; $p < 0.0001$). November 1998 was the month with the biggest catch, followed by
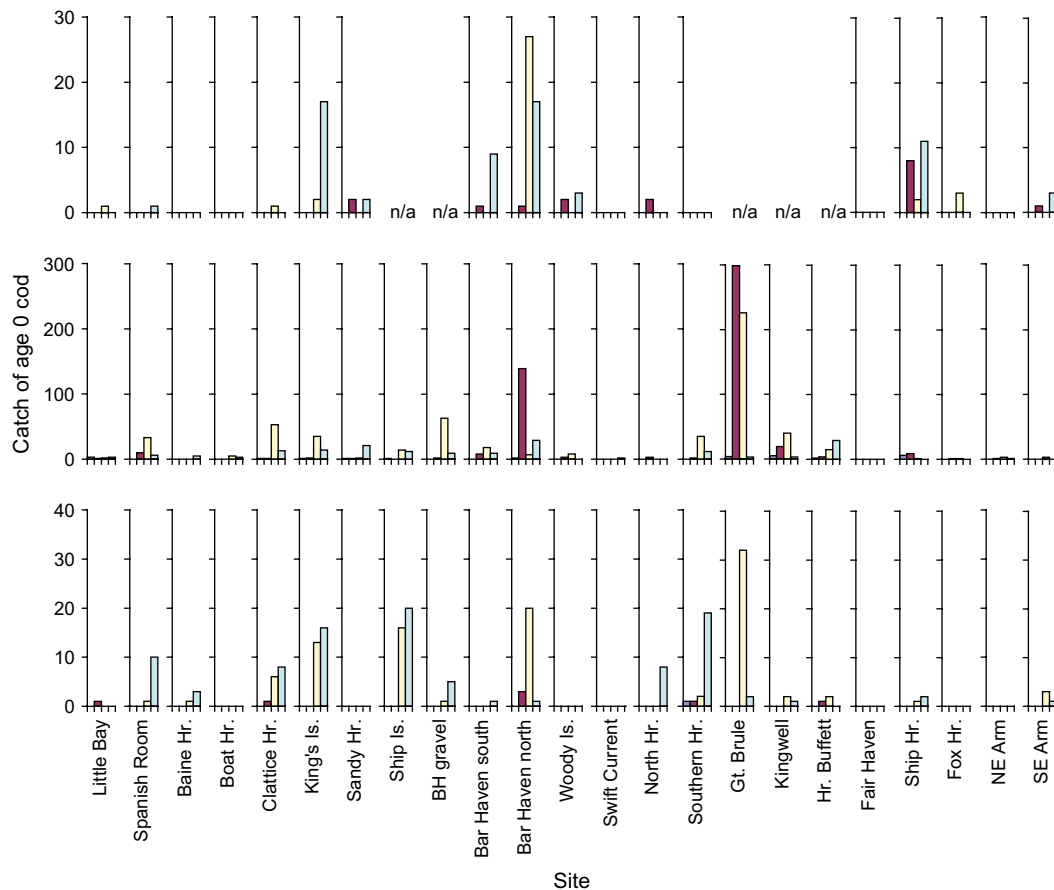
Figure 2. Location and catch of age 0 cod at each of the 23 Placentia Bay sampling sites, listed in an order approximating west to east travel around the perimeter of the bay. The bars represent catch (in number of fish) for September (leftmost bar), October (second bar), November (third bar), and December (rightmost bar). The top, middle, and bottom rows of graphs show data from 1997, 1998, and 1999, respectively. Note that five of the 23 sites were not sampled in 1997.

October, then December. In 1997 and 1999, the catches increased continuously from September to December (Figure 3).

For the five newer sites, the negative binomial parameter was not a function of MONTH in 1999 (Dev = 0.6; d.f. = 3; $p = 0.90$), and the model was therefore simplified to include only one value of $k$. However, the data from 1998 could not be simplified in this way (Dev = 7.8; d.f. = 3; $p = 0.050$). Regardless, there was a strong effect of MONTH within both years (1998: Dev = 26.3; d.f. = 6; $p < 0.001$. 1999: Dev = 18.2; d.f. = 3; $p < 0.0001$). At these five newer sites, catch rates peaked in November in both 1998 and 1999, but in the former year, October and December catches were substantial, while October catches in the latter year were poor (Figure 3).

Overall, the models using the negative binomial error structure performed well. The modelled mean values were strongly correlated with the observed mean catch values ($r = 0.96$; $p < 0.0001$; Figure 3).

The mean length of age 0 cod caught in Placentia Bay varied over time within each year (Figure 4). During the early parts of each survey year, average lengths increased with time. However, towards the end of each year, the larger fish were not caught, and catches became dominated by smaller (<45 mm) cod.

## Density-dependent distribution

The distribution of age 0 cod in Placentia Bay appeared to show density-dependence. As the number of cod caught in a given month (i.e. the total cod caught at all study sites) increased, so did the number of sites at which cod were present [Figure 5; proportion of sites with cod = $-0.031 + 0.13 \times \ln$ (abundance); $r^2 = 0.95$; the slope was significantly different from zero ($t = 13.4$; $p < 0.0001$)]. The asymptotic relationship was linearized by ln-transforming abundances. The response variable was presented as proportions of the total

Table 1. Modelled catch estimates for effect of SITE on age 0 cod catch in 1997 (144 beach-seine hauls at 18 locations) and between 1998 and 1999 (368 beach-seine hauls at 23 locations over two years). Means and 95% confidence limits result from bootstraps of the simplified model.

| Parameter | 1997 | | 1998−1999 | |
| --- | --- | --- | --- | --- |
| | Catch mean | Confidence limits | Catch mean | Confidence limits |
| Baine Hr. | 0.0 | 0.0−0.0 | 0.4 | 0.4−0.5 |
| Bar Haven gravel site | − | − | 4.2 | 3.1−5.5 |
| Bar Haven North | 4.6 | 2.1−10.2 | 10.3 | 7.8−13.7 |
| Bar Haven South | 0.6 | 0.2−1.7 | 2.1 | 1.6−2.8 |
| Boat Hr. | 0.0 | 0.0−0.0 | 0.2 | 0.1−0.4 |
| Clattice Hr. | 0.0 | 0.0−0.0 | 4.0 | 3.0−5.5 |
| Fair Haven | 0.0 | 0.0−0.0 | 0.0 | 0.0−0.0 |
| Fox Hr. | 0.0 | 0.0−0.0 | 0.0 | 0.0−0.0 |
| Great Brule | − | − | 25.4 | 18.5−34.9 |
| Hr. Buffett | − | − | 2.9 | 1.4−6.2 |
| King's Is. | 1.3 | 0.5−3.5 | 4.8 | 3.6−6.3 |
| Kingwell | − | − | 3.9 | 3.0−5.2 |
| Little Bay | 0.0 | 0.0−0.0 | 0.3 | 0.2−0.4 |
| North Hr. | 0.0 | 0.0−0.0 | 0.3 | 0.2−0.5 |
| Northeast Arm | 0.2 | 0.0−1.7 | 0.3 | 0.2−0.6 |
| Sandy Hr. | 0.0 | 0.0−0.2 | 1.2 | 0.8−1.6 |
| Ship Hr. | 1.4 | 0.2−8.4 | 1.1 | 0.8−1.4 |
| Ship Is. gravel site | − | − | 3.6 | 2.7−4.8 |
| Southeast Arm | 0.0 | 0.0−0.0 | 0.5 | 0.4−0.7 |
| Southern Hr. | 0.0 | 0.0−0.0 | 3.9 | 3.0−5.2 |
| Spanish Room | 0.0 | 0.0−0.0 | 3.5 | 2.6−4.6 |
| Swift Current | 0.0 | 0.0−0.0 | 0.0 | 0.0−0.0 |
| Woody Is. | 0.4 | 0.2−1.0 | 0.4 | 0.2−0.6 |

number of sites examined to account for the increase in number of study sites in 1998.

## Discussion

The catch rates of age 0 cod were low in 1997 and 1999 (0.8 and 1.1 fish per haul, respectively) despite evidence of relatively high levels of spawning within the bay in both years (Bradbury *et al.*, 2000; Lawson and Rose, 2000a; GAR, unpublished data). Only in 1998, when the overall catch was 6−8 times greater than in the other years, did catch rates (6.9 fish per haul) resemble those reported from other Newfoundland bays. Average late September to late October catch rates for other Newfoundland bays during recent years (1992−1995) ranged from 1.8 fish per haul in St Mary's Bay to 45 fish per haul in Bonavista Bay (Smedbol *et al.*, 1998). Concurrent to this study (1997), a survey of northeastern Newfoundland bays showed mean catch rates ranging from 1.7 fish per haul in Conception Bay to 75.5 fish per haul in Trinity Bay (this latter value is likely not representative of other northeastern coast sites because Trinity Bay is home to the Smith

Sound spawning cod aggregations; see Rose, 2003), whereas in St Mary's Bay, the only other South Coast bay surveyed, catch rates were 4.4 cod per haul (Methven *et al.*, 1998). Given the timing of the surveys of the other Newfoundland bays, it might be appropriate to compare them only with the September and October catches of the current study. However, doing so would result in relatively lower catch rates for Placentia Bay, because September was poor in comparison with other months, and November was consistently the peak month for age 0 cod catches. Methven and Bajdik (1994) found the peak period of juvenile cod in Trinity Bay to be somewhat earlier than in Placentia Bay (August−November).

One explanation for these apparent differences between Placentia Bay and other Newfoundland bays is that Placentia is primarily a source of juveniles, whereas those on the northeast coast are primarily receivers of juveniles spawned either offshore (Anderson and Rose, 2001), or inshore (especially in Trinity Bay, where the large Smith Sound cod aggregation spawns; Smedbol and Wroblewski, 1997; Rose, 2003). Consistent with this notion, residual current flows, which would substantially influence the drift of eggs and larvae, are seawards out of Placentia Bay, in a counter-clockwise gyre, but shorewards into the bays of the northeast coast. The extent of the distribution of juvenile cod spawned in Placentia Bay is not known. However, there are no shoreward flows from the offshore spawning sites south of Placentia Bay, so few eggs or larvae are brought near to shore (as occurs on the northeast coast, Bradbury *et al.*, 2000). In contrast, Placentia Bay current patterns would be expected to carry eggs westwards towards Burgeo Bank, or to cause them to be entrained in the flows associated with St Pierre Bank.

The sites in the northern part of the bay (especially Bar Haven and Great Brule) generally yielded larger catches of age 0 cod than those in other parts of the bay. This is likely to have resulted from the spawning observed near Bar Haven in all years studied. Local retention of eggs and larvae is likely in the Bar Haven area. Drifters released at Bar Haven during the 1997 spawning season were most often recovered among the islands in the northern part of the bay, and along the west coast of Merasheen Island (Bradbury *et al.*, 2000), matching the distribution of age 0 juveniles described in this study. Retention of eggs and larvae in the northern part of the bay is consistent with the variable and relatively weak currents (Schillinger *et al.*, 2000), complex bottom topography (as per Mullineaux and Mills, 1997), and the presence of many small islands, particularly on the western side of the bay. The interannual variation in juvenile density in relation to spawning densities and resultant recruitment to the adult spawning population is currently under study.

The rank of the sites from greatest to least age 0 cod density remained fairly consistent among years. For example, catches at Great Brule and Bar Haven North were consistently greater than at any others in the bay. This
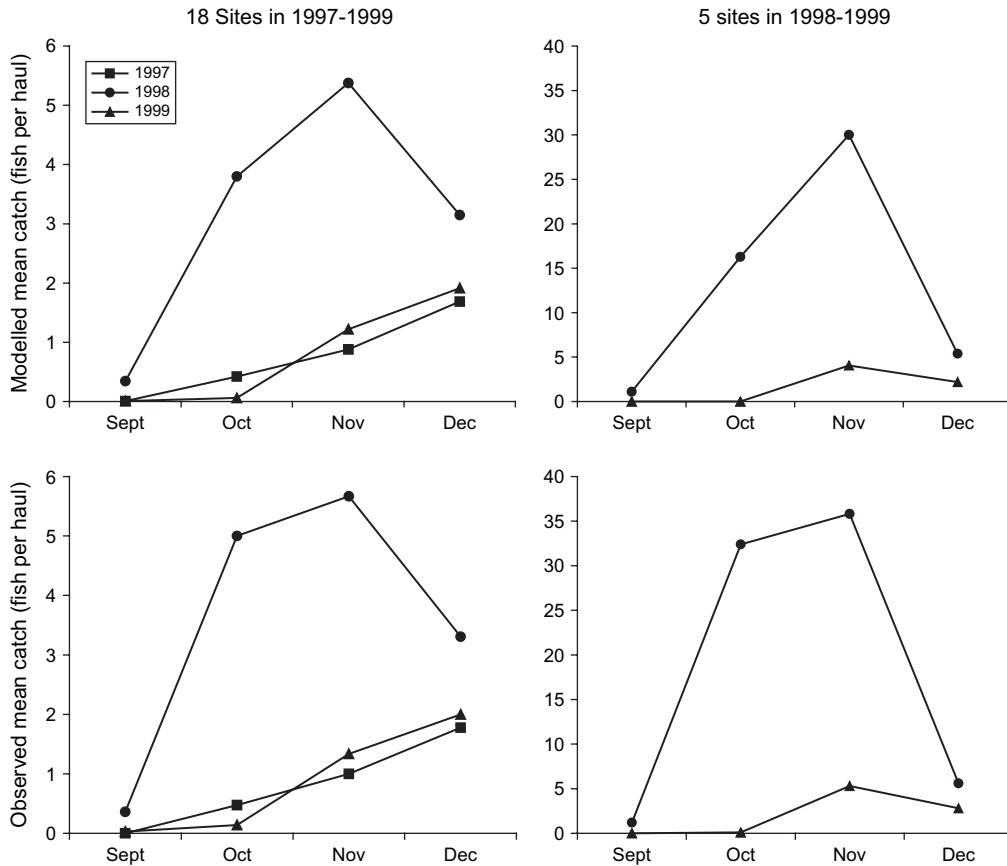
Figure 3. The modelled (upper panels) and observed (lower panels) mean catch rates by month for the three study years. The results using data from the 18 main sites are shown in the leftmost panels, whereas the rightmost panels show data from the five sites that were newly added in 1998.

inter-year consistency of ranked catches (and possibly of quality) among sites allows identification of nursery grounds within the bay. However, our data indicate that as abundance of demersal juveniles increases, there is a concomitant decline in the relative importance of these sites, as a consequence of an expansion of cod presence across a greater number of sites.

Our data show that age 0 cod occupy a greater number of sites when abundance is greater. As the number of cod caught in a given month increased, so did the number of sites occupied by cod. The asymptotic relationship indicated that the proportion of sites used by cod increased much less rapidly than did abundance. Hence, some sites might only be used in years of very high abundance of juvenile cod. We caution that there is autocorrelation in the relationship (presence of cod, $y$, is a function of the number of cod, $x$), making the exact $p$ values of this relationship questionable. However, the autocorrelation would be zero under a scenario of increasing abundance without an increase in number of occupied sites (all additional cod go to sites already occupied). Therefore, with increasing degrees of density-dependent range fluctuation, there must

be increasing autocorrelation. As such, the degree of autocorrelation is the test of interest, not an artefact of it. For Placentia Bay cod, the relationship was very strong, showing a clear density-dependent effect. At low numbers, only a few sites were occupied, but as the number of individuals increased, more sites were occupied.

This is not the first study to find density-dependence in Atlantic cod. Rose and Leggett (1991) found that biomass of adult Gulf of St Lawrence cod was positively correlated with range occupied. Swain and Wade (1993) found that the geographic range of southern Gulf of St Lawrence cod 3–8 years old also increased with abundance. Our results expand on previous reports, by demonstrating that density-dependent effects occur in young-of-the-year demersal cod. Interestingly, it was only for the youngest cod tested (age 3) by Swain and Wade (1993) that the areas of greatest density were the same at low and high levels of abundance. For age 4–8 cod, the areas of greatest density shifted with levels of abundance. In the present study, age 0 cod behaved more similarly to age 3 cod than to older conspecifics.

Density-dependence of behaviour has been previously demonstrated for age 0 Atlantic cod. Laurel *et al.* (2004)
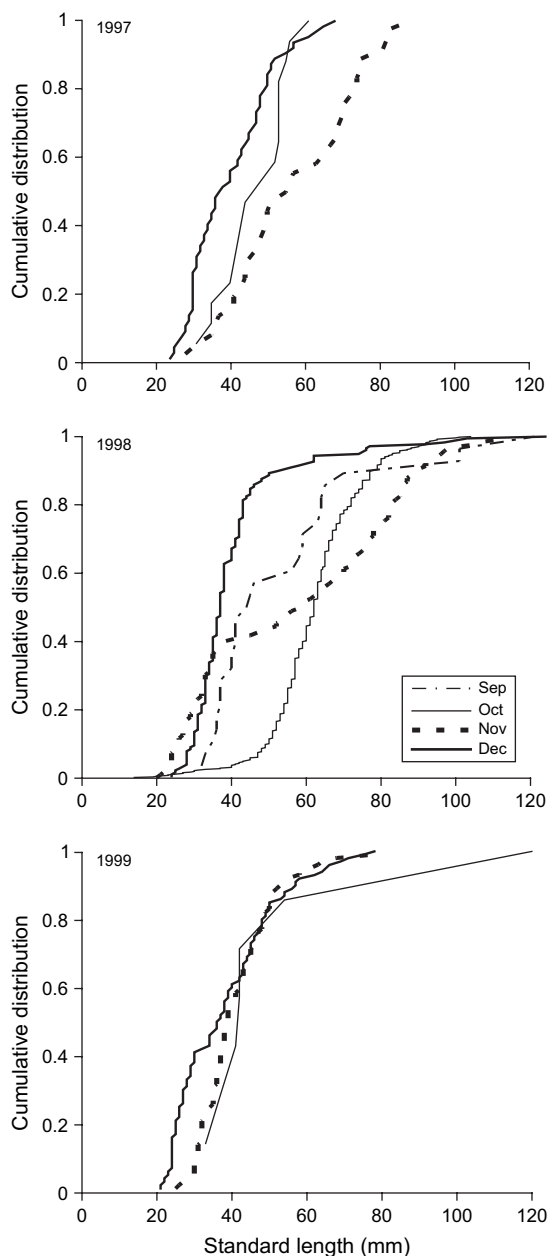
Figure 4. Cumulative relative frequency of standard lengths of age 0 cod for each of the four monthly surveys in 1997 through 1999. Note that no age 0 cod were caught in September 1997, and only one was caught in September 1999.
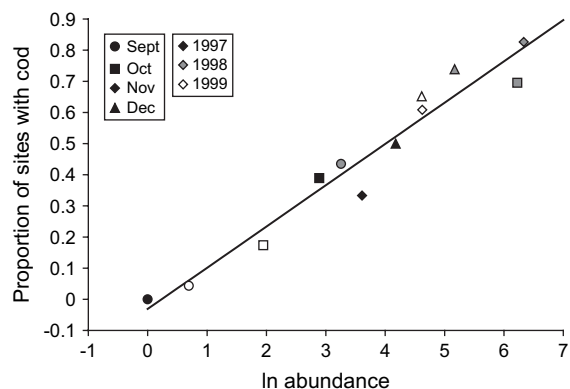


Figure 5. Distribution expansion with abundance. Proportion of total number of sites surveyed that had age 0 cod in the catch, plotted against the natural logarithm of the overall abundance (total number of age 0 cod caught at all study sites) in the bay. Each point represents one survey month. The line is a standard least squares regression $y = -0.031 + 0.13x$ ($r^2 = 0.95$). Symbols: shapes correspond to sampling months, and shades indicate sampling years.

similar effects in pollock (*Pollachius virens*), and suggested that they result from a shift in optimal anti-predator tactics at higher overall abundances.

It is interesting and contradictory to the present results that Schneider *et al.* (1997) did not find evidence of density-dependent range fluctuation in age 0 cod along the northeast coast of Newfoundland. However, the geographic scale of that work was large relative to the present study, and supply differences among different parts of the northeast coast could have confounded their results (see Mac-Call, 1990; Shepherd and Litvak, 2004). The northeast coast has several potential sources of juveniles. There are coastal spawning groups (Rose, 2003) and several offshore Bank groups (Rose, 1993; Anderson and Rose, 2001). All likely contribute juveniles to the coastal zone. Unfortunately, the origins of the juveniles under study on the northeast coast have never been known. Such confounding of any density-dependence is thought to be far less likely at the smaller scale of Placentia Bay, where drift of eggs and larvae into the bay is *a priori* less likely, and was near zero during the years of the present study (Bradbury *et al.*, 2000). Although we cannot prove that the juveniles observed in this study were spawned within Placentia Bay, the weight of the spatial and temporal evidence of spawning within the bay (Lawson and Rose, 2000a, b), distributions of eggs and larvae (Bradbury *et al.*, 2000), and the lack of any apparent external sources, all suggest that they were. The settling of juveniles outside the bay (and the boundaries of the present study) must remain speculative, but might expand the range of this population even further at higher densities.

The mechanism by which cod in this study achieved the observed density-dependent range dynamics is not known. We cannot assume habitat selection (as per Shepherd and Litvak, 2004). When there are more eggs and larvae, they

found that cod modified their habitat use with changing density. In all years of their study, cod were most likely to be found in eelgrass habitats, but in years of greater overall abundance, high density aggregations were observed over unvegetated habitat. Those authors suggested that the behavioural change was a means of exploiting poorquality habitats when high-quality ones were saturated with conspecifics. Rangeley and Kramer (1998) observed

might simply become more widely dispersed. As pointed out by Shepherd and Litvak (2004), density-dependent habitat selection requires informed decisions about the quality of widely distributed habitats, well outside the experience of an individual young cod, and with significant costs to gaining that information. If cod eggs and larvae are swept away from the prime sites, even out of the bay, they can hardly be considered to have made a choice. On the other hand, it may only be those that drift to the prime areas that survive. Neither can we dismiss the possibility that sites occupied at low abundance may be of superior quality (either as a consequence of their location, or as a result of their physical and biological properties), and that range expansion at larger numbers occurs into suboptimal habitats (MacCall, 1990). Consistent with this notion is the observation that the sites that held the most juvenile cod were the same in years of both local scarcity and abundance. If correct, then these sites would represent the most critical habitat for juvenile cod in Placentia Bay. At present, we cannot differentiate between habitat selection and environmental affects on distribution as mechanisms underlying the density-dependence of juvenile cod observed in this study. However, we agree with Shepherd and Litvak (2004) that resolution of these issues remains a central question in marine fish ecology and of prime importance to conservation and management.

## Acknowledgements

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